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# Potential distribution and habitat connectivity of *Crotalus triseriatus* in Central Mexico

## Potentielle Verbreitung und Habitatkonnektivität von *Crotalus triseriatus* in Zentralmexiko

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## Abstract

The dusky rattlesnake, *Crotalus triseriatus*, used to be very abundant in many parts of the highlands of central Mexico, but with the increasing human population and associated activities, the rattlesnake habitats and populations have suffered drastic reductions and fragmentation. At the moment, the most important habitat features, associated with the presence of *C. triseriatus*, the current potential distribution and the landscape connectivity amongst the populations of the State of Mexico and Mexico City, are unknown. Therefore, we used the maximum entropy modelling software (MAXENT) to analyse the current potential distribution and most important habitat features, associated with the presence of the species. The variables with the highest contribution to the model were: proportion of *Abies* forest, minimum temperature of coldest month, maximum temperature of the warmest month, proportion of *Pinus* forest and annual precipitation. Furthermore, we found connectivity corridors only within mountain chains. Our results highlight the necessity for conserving the patches of *Abies* forest and preserving the populations of *C. triseriatus* and the connectivity of the landscape.

## Kurzfassung

Früher war *Crotalus triseriatus* in vielen Teilen des Hochlandes von Zentralmexiko häufing, aber mit der wachsenden Bevölkerung und den damit verbundenen Aktivitäten haben die Lebensräume und die Populationen der Klapperschlangen drastische Rückgänge und Fragmentierungen erfahren. Derzeit wissen wir nicht, welche Habitatmerkmale am wichtigsten für das Auftreten von *C. triseriatus*, seine aktuelle potentielle Verbreitung und die landschaftlichen Konnektivität zwischen den Populationen des Staates Mexiko und Mexiko- Stadt sind. Aus diesem Grund haben wir die Maximum-Entropy-Modellierungssoftware (MAXENT) verwendet, um die aktuelle potenzielle Verbreitung und die wichtigsten Habitatmerkmale zu ermitteln, die mit dem Vorkommen der Art zusammenhängen. Die Variablen mit dem höchsten Beitrag zum Modell waren: Anteil des *Abies*-Waldes, minimale Temperatur des kältesten Monats, maximale Temperatur des wärmeren Monats, Anteil des *Pinus*-Waldes und jährlicher Niederschlag, und wir fanden Verbindungskorridore nur innerhalb von Gebirgsketten. Als Fazit ist es notwendig, die Bestände des *Abies*-Waldes und die Populationen von *C. triseriatus* und die Konnektivität der Landschaft zu erhalten.

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Key Words

circuit theory, ecological niche modelling, habitat fragmentation, habitat suitability, protected natural areas

# Introduction

The conservation and management of species require basic information on their geographic distribution, ecology and abundance of populations. In recent years, ecological niche modelling (ENM) has been widely used to assess geographic distribution of species at different scales for conservation purposes, with reliable results (Peterson et al. 2011). Additionally, ENM allows the inference of the environmental requirements from occurrence data and the understanding of the basic aspects of the biology of the species that are difficult, sometimes impossible, to address using other methods (Warren and Seifert 2011).

Rattlesnakes are abundant in many parts of Mexico and have a wide distribution spread around the country (Campbell and Lamar 2004). The dusky rattlesnake, *Crotalus triseriatus*, is found in the grasslands of highlands of central Mexico along the Trans-Mexican Volcanic Belt (TMVB, Fig. 1A), at very high altitudes of about 4,572 metres above mean sea level (AMSL). However, it is most common at 2,700 to 3,350 AMSL (Campbell and Lamar 2004; Fernández-Badillo et al. 2011). This species is diurnally active and is mainly found in *Pinus-Quercus* forests, grasslands and agricultural areas (Canseco-Márquez and Mendoza-Quijano 2007; Fernández-Badillo et al. 2011). It is classified as Least Concern on the IUCN Red List due to its wide distribution and presumed large population, but this assignment may be due to a lack of knowledge on the natural history of the species (Canseco-Márquez and Mendoza-Quijano 2007; Bryson et al. 2014; Sunny et al. 2015). The few ecological studies on this species are very basic, only reporting localities of presence, types of habitat where the species was found, size of the snakes and diet of the species. (Mociño-Deloya et al. 2014; Domínguez-Guerrero and Fernández-Badillo 2016). Hence, it is necessary to enhance the information about this species dynamics and habitat to improve and optimise conservation efforts.

Most populations of *C. triseriatus*, as well as other species of this group, have declined due to urban development, hunting and habitat loss (Campbell and Lamar 2004). The distributional range of *C. triseriatus* presents strong anthropogenic transformation of the ecosystems; approximately 73.4% of this area has experienced this type of disturbance (cities, agriculture and roads) and in 2013 only 1.1% of *Abies* forest and 5.4% of *Pinus* forest remain (Sunny et al. 2017; González-Fernández et al. 2018). These anthropogenic transformations of the ecosystem could increase the extinction risk of *C. triseriatus* due to the loss and fragmentation of its habitat. Along with this, the restricted vagility of the snakes (Macartey et al. 1988; Sasa et al. 2009; Hoss et al. 2010) could have long-term consequences, such as a decrease in genetic diversity and an increased chance of inbreeding and proliferation of disease (Guthrie et al. 2015; Tetzlaff et al. 2015; Glorioso et al. 2016). Therefore, habitat transformation is highly important to *C. triseriatus* populations because these species are more vulnerable due to their small home ranges, high philopatry and low vagility (Huey 1982; Anadón et al. 2006; Castellano and Valone 2006; Ribeiro et al. 2009; Sunny et al. 2019).

In order to propose conservation strategies for *C. triseriatus*, it is essential to address the environmental requirements and precise distribution of *C. triseriatus*, as well as the degree of fragmentation of their habitats. Consequently, our research questions are: 1) what are the environmental requirements of *C. triseriatus;* 2) which are the most important habitat features associated with the presence of the species; 3) what is the current potential distribution of *C. triseriatus* in central Mexico; and finally, 4) what is the degree of landscape connectivity amongst populations of *C. triseriatus* in the State of Mexico and Mexico City? These results will provide valuable information for management decisions orientated towards helping to preserve this endemic species.

# Material and methods

## Study area and population sampling

Field work was conducted at 24 sites in the State of Mexico and Mexico City (Fig. 1B). During the period from 2012 and 2014, we performed 24 monthly visits to each study site. When a *C. triseriatus* was observed, we recorded general habitat notes, date, location and geographic coordinates (GPS) with a WGS 84 datum. The field survey was conducted with the approval of the ethics committee of the Autonomous University of the State of Mexico (DCARM-2014; 9855714) and with the field permit: SGPA/DGVS/011587/17 SEMARNAT). During each visit, two observers simultaneously walked two 2 km long transects from 09:00 to 17:00 h, which were separated by 200 to 300 m. We randomly placed transects to ensure that they covered all types of vegetation in a similar proportion to their presence.

## Ecological niche modelling and landscape connectivity

For ENM, a database of records on the geographical distribution of the species was compiled. After an auto-

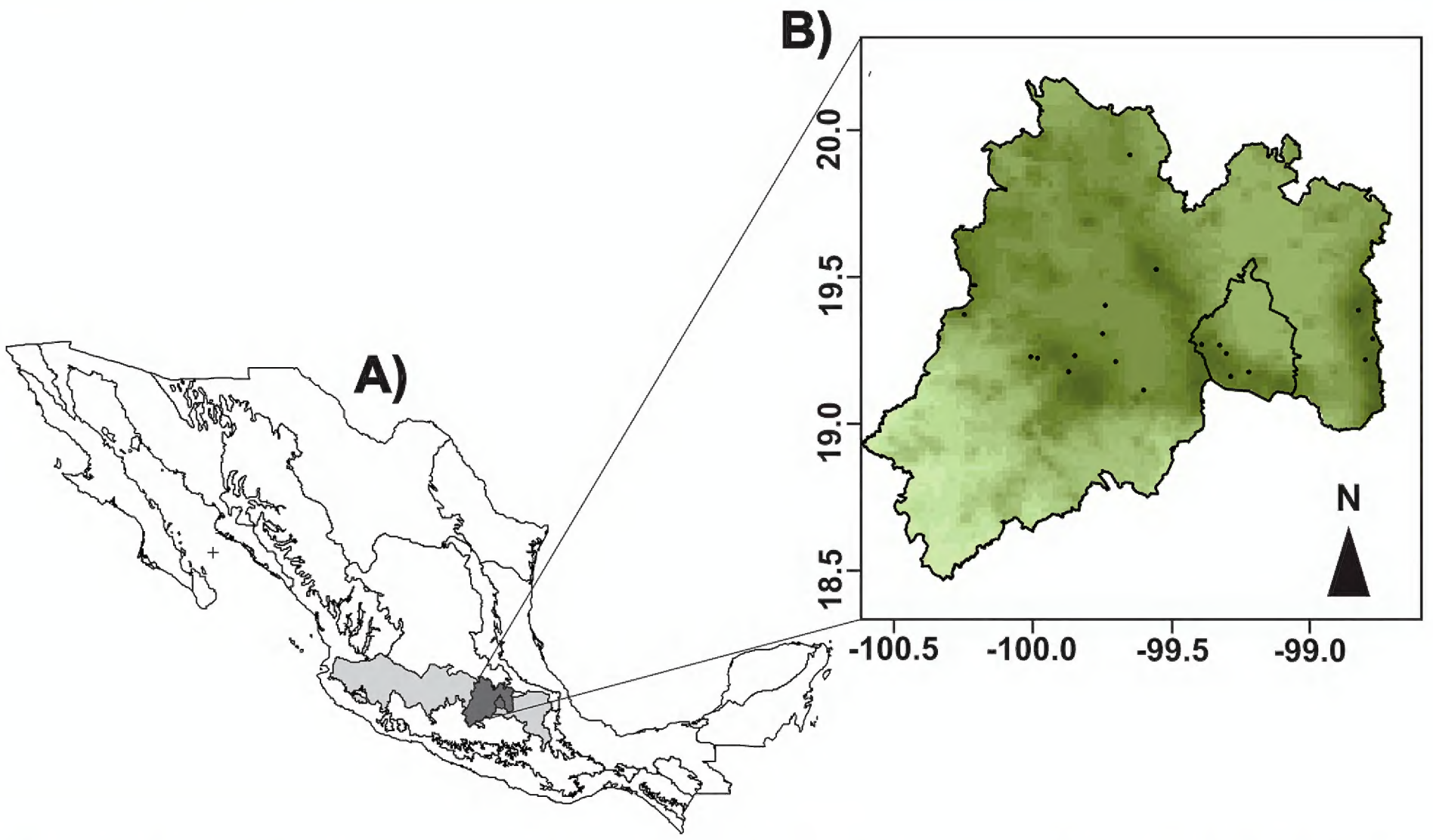


**Figure 1. A)** Map of Mexico showing the Trans-Mexican Volcanic Belt, the State of Mexico and Mexico City. **B)** Map of the State of Mexico and Mexico City where the sampling sites are shown in an elevation raster, the darker areas refer to high elevation.

correlation test using the software NICHE TOOLBOX (Osorio-Olvera et al. 2016) for R software (version 3.4.0; R Development Core Team 2017), we discarded highly correlated variables ($R^2 > 0.7$, Dormann et al. 2013), of an original set of 30 variables. We considered the inclusion of 14 environmental and human-induced alteration variables (Table 1; scale of 1:250,000; INEGI 2013), which are recognised as important for determining the presence of *C. triseriatus* (Campbell and Lamar 2004). All variables were continuous and represent proportions of this habitat in relation to a 1×1 km cell. We only worked with two distance variables, which were: distance to human settlements and distance to water sources. We obtained a digital map of land cover from the National Institute of Statistics and Geography (INEGI 2013). This map is the result of derived layers from Landsat TM5 satellite images integrated with local fieldwork (series V INEGI 2013). All layers were processed in a raster format, with 1 km resolution, using ARCGIS 10.5 and the packages TIFF (Urbanek 2015), RASTER (Hijmans 2016) and RGDAL (Bivand and Keitt 2015) for R. We obtained the temperature and precipitation variables from the WorldClim database (Hijmans et al. 2005); altitude information was available through the USGS/NASA Shuttle Radar Topography Mission (USGS 2007).

We applied the Maximum Entropy algorithm using MAXENT software (Phillips et al. 2006). We ran the model in MAXENT with 10 bootstraps replicates with 75–25% for training and testing, respectively (Anderson et al. 2003; Chefaoui et al. 2005; Suárez-Atilano et al. 2017). We only used linear and quadratic features due to low sample size (Merow et al. 2013). All analyses were performed with a convergence threshold of $1 \times 10^{-5}$ with 500 iterations (Pearson 2007; González-Fernández et al. 2018). We used two approaches to evaluate overall classification accuracy in the model: first, the scores from the area under the curve (AUC) from the receiver operating characteristic plot (Metz 1978; Phillips et al. 2006) and second, the transformation of AUC into partial-ROC graphics (Peterson et al. 2008). We used the software NICHE TOOLBOX for partial-ROC calculations. We generated the species potential distribution binary maps using Max SS threshold (Liu et al. 2013), a threshold selection method based on maximising the sum of sensitivity and specificity. This is considered an adequate method to use when reliable absence data are unavailable (Liu et al. 2013).

For the landscape connectivity, we modelled patterns of population connectivity using circuit theory, where population connectivity is analogous to an electrical current (McRae 2006; McRae et al. 2008; Garrido-Garduño et al. 2016). The model uses a graph-theoretical approach to predict movement patterns and quantify the effects of landscape features, where the distance metric is the total resistance value across the entire surface (Garrido-Garduño et al. 2016). The ENM map was used as an input for the software CIRCUITSCAPE 4 (McRae et al. 2013) to generate spatial resistance distances to dispersal amongst sites based on habitat suitability maps (Velo-Antón et al. 2013). The CIRCUITSCAPE software calculates pairwise resistances to gene flow amongst populations based on all

**Table 1.** Habitat variables in percentage of habitat in a 1×1 km cell, considered for the ENM and landscape connectivity resistance map.

| Variable | Units | Source | Author(s) | Year |
|---|---|---|---|---|
| Proportion of agriculture | % | National forest inventory | INEGI | 2013 |
| Proportion of cloud forest | % | National forest inventory | INEGI | 2013 |
| Proportion of *Abies* forest | % | National forest inventory | INEGI | 2013 |
| Proportion of *Quercus* forest | % | National forest inventory | INEGI | 2013 |
| Proportion of *Quercus-Pinus* forest | % | National forest inventory | INEGI | 2013 |
| Proportion of *Pinus* forest | % | National forest inventory | INEGI | 2013 |
| Proportion of *Pinus-Quercus* forest | % | National forest inventory | INEGI | 2013 |
| Proportion of grassland | % | National forest inventory | INEGI | 2013 |
| Distance to water sources | km | National forest inventory | INEGI | 2013 |
| Distance to settlements | km | National forest inventory | INEGI | 2013 |
| Altitude | MASL | Digital elevation model | USGS | 2007 |
| Annual precipitation | mm | WorldClim | Hijmans et al. | 2005 |
| Maximum temperature of the warmest month | °C | WorldClim | Hijmans et al. | 2005 |
| Minimum temperature of the coldest month | °C | WorldClim | Hijmans et al. | 2005 |

**Table 2.** Average contribution percent of variables according MAXENT, the Interval of occurrence that explain the distribution of *C. triseriatus* and the standard deviations of the contribution percent of variables according MAXENT.

| Variable | Contribution to the model | Interval of *C. triseriatus* occurrence | Standard deviation |
|---|---|---|---|
| *Abies* forest | 25.1% | 10–90% | 0.069 |
| Minimum temperature of coldest month | 19.6% | -1–12 °C | 0.351 |
| Maximum temperature of the warmest month | 17.1% | 5–27 °C | 0.104 |
| *Pinus* forest | 13.3% | 10–100 % | 0.041 |
| Annual precipitation | 8.3% | 500–1600 mm | 0.336 |
| *Pinus-Quercus* forest | 6.7% | 10–100 % | 0.051 |
| Altitude | 4.1% | 2000–4600MASL | 0.262 |
| Distance to settlements | 3.4% | 0–32.5 km | 0.046 |
| *Quercus* forest | 1.6% | 0–30% | 0.263 |
| Distance to water sources | 0.3% | 0–28 km | 0.106 |
| Grassland | 0.2% | 0–90% | 0.102 |
| Cloud forest | 0.2% | 0–65% | 0.274 |
| Agriculture | 0% | 0–95% | 0.116 |
| *Quercus-Pinus* forest | 0% | 0–100% | 0.268 |

possible paths, not just the path with the lowest cost, thus better explaining the movement of genes amongst widely separated regions over many generations (McRae and Beier 2007; McRae et al. 2008; Velo-Antón et al. 2013). Each calculation used focal points in pairwise mode between *C. triseriatus* populations and a four-neighbour connection scheme that allowed gene flow amongst the four nearest cells.

## Results

For the ENM, we obtained 24 records (Fig. 1), including fifteen in the State of Mexico and nine in Mexico City.

The MAXENT model performed better than expected by random, where the AUC showed high average values across iterations (AUC = 0.990 P = 0.001). Additionally, the partial-ROC bootstrap test showed significant ratio values of empirical AUC over null expectations (ratio = 1.437; P = 0.001). The model (Fig. 2) predicts that the highest probability of presence of *C. triseriatus* is found in the mountain ranges of the State of Mexico and Mexico City, mainly in the Iztaccíhuatl-Popocatépetl-Zoquiapan (Fig. 2, number 1), Sierra de las Cruces (Fig. 2, number 2), the Corredor Biológico Chichinautzin (Fig. 2, number 3), the Nevado de Toluca Volcano (Fig. 2, number 4) and Reserva de la Biósfera Santuario Mariposa Monarca (Fig. 2, number 5), although there is also a probability of presence in lower areas of the State of Mexico and Mexico City.

The variables with the highest contribution to the model were: *Abies* forest, minimum temperature of the coldest month, maximum temperature of the warmest month, *Pinus* forest and annual precipitation; together, these variables explained 83.4% of the variation in species distribution (Table 2 and Fig. 3). The probability of presence of *C. triseriatus* is 78% when there are few *Abies* forest areas up to 40%, then it decreases to 73% the probability of presence of *C. triseriatus* when there are 50% to 90% of *Abies* forest areas (Table 2; Fig. 3A). There was a positive linear correlation between the proportion of *Pinus* forests and the probability of presence of the species in an interval of 10–100% of *Pinus* forests (Table 2; Fig. 3D); the probability of presence related to the minimum temperature of the coldest month was highest at temperatures ranging from -1 °C to 12 °C (Table 2; Fig. 3B), the probability of presence related to the maximum temperature of

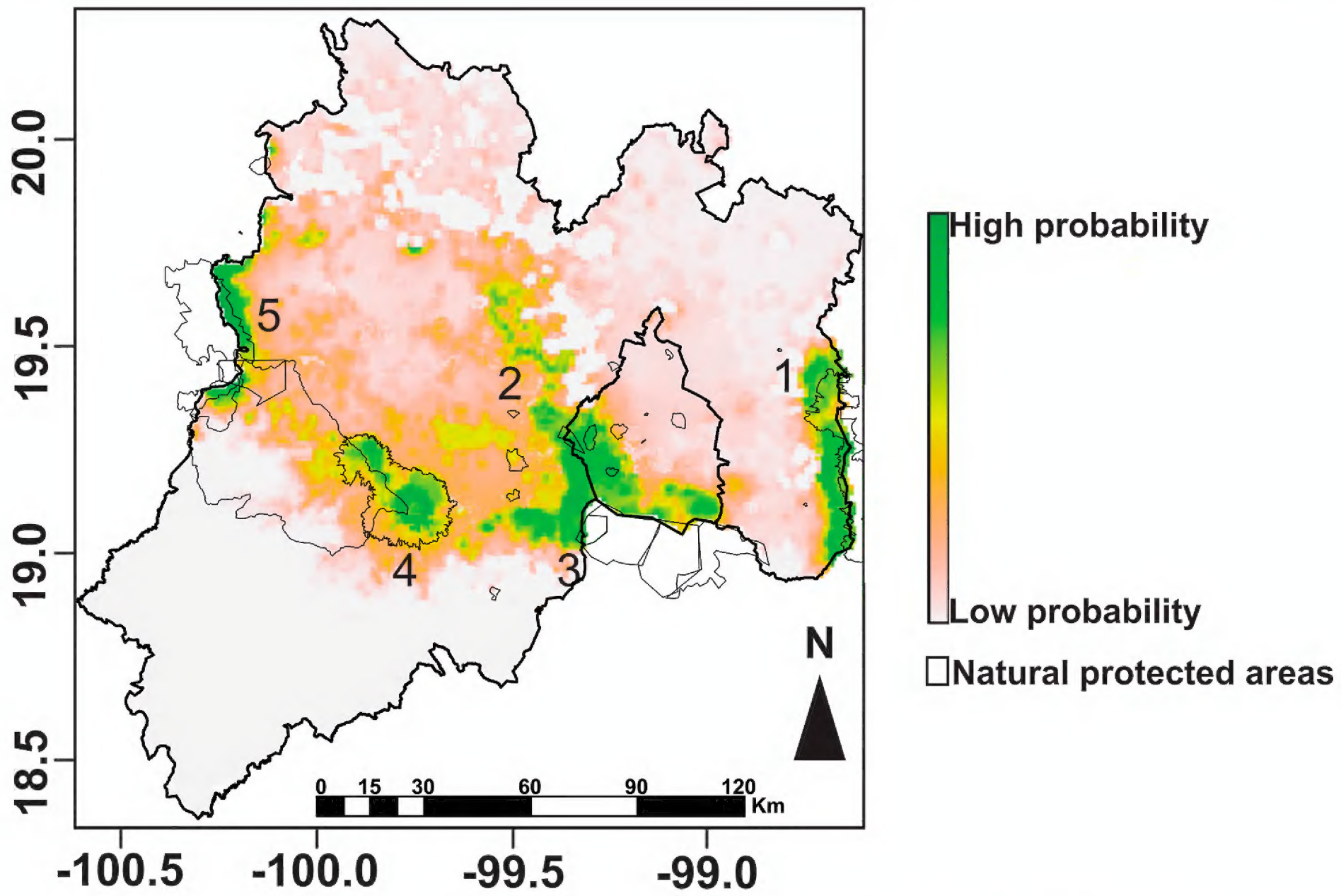


**Figure 2.** Potential distribution of *C. triseriatus* identified using ENM in the State of Mexico and Mexico City. **1.** Iztaccíhuatl-Popocatépetl-Zoquiapan, **2.** Sierra de las Cruces, **3.** The Corredor Biológico Chichinautzin, **4.** The Nevado de Toluca Volcano and **5.** Reserva de la Biósfera Santuario Mariposa Monarca.

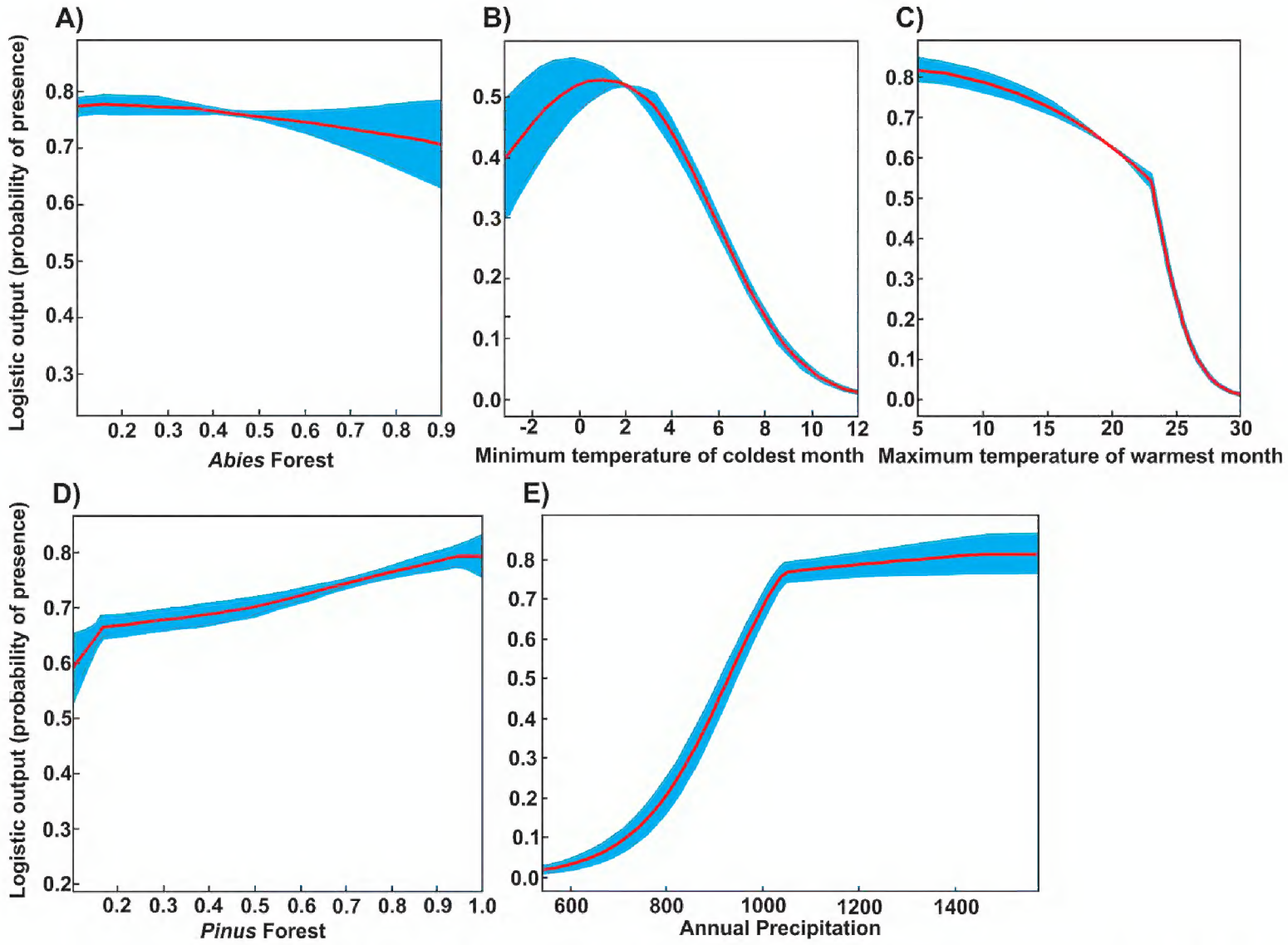


**Figure 3.** Variables with the highest contribution to the potential distribution of *C. triseriatus* according to MAXENT with the standard errors in blue. In the Y axis is the probability of presence and in the X axis de contribution of each variable.

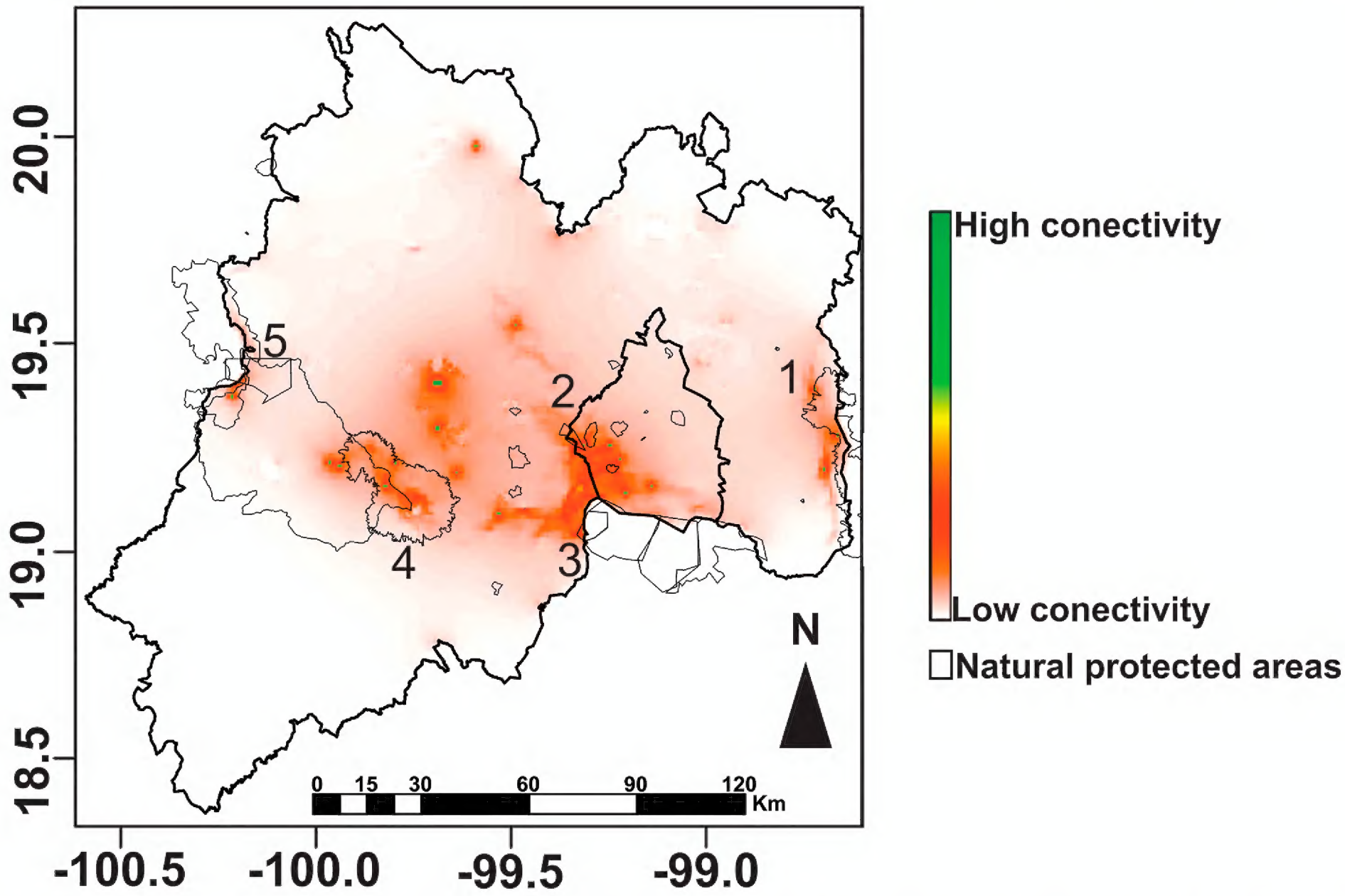


**Figure 4.** Connectivity maps among 24 studied sites for *C. triseriatus*. The resistance map was estimated using CIRCUITSCAPE and based on habitat suitability from ENM reconstructions. Red and green indicates areas with higher current density; areas where connectivity is most tenuous are shown in lighter oranges. **1.** Iztaccíhuatl-Popocatépetl-Zoquiapan, **2.** Sierra de las Cruces, **3.** The Corredor Biológico Chichinautzin, **4.** The Nevado de Toluca Volcano and **5.** Reserva de la Biósfera Santuario Mariposa Monarca.

the warmest month was highest in the temperature range from 5–27 °C (Table 2; Fig. 3C) and the species was shown to occur in areas with annual precipitation ranges from 500–1600 mm (Table 2; Fig. 3E). The whole study area includes 10,577.799 km$^2$ of agriculture, 1,705.116 km$^2$ of urbanisation, 2,816.074 km$^2$ of *Pinus* forest and 863.913 km$^2$ of *Abies* forest and shares an area of potential distribution of *C. triseriatus* of 10,526.012 km$^2$.

ENM resistance surfaces showed connectivity corridors principally within mountain chains (Fig. 4). The mountain chains with the major connectivity corridors between populations were Sierra de las Cruces (Fig. 4, number 2) and the Corredor Biológico Chichinautzin (Fig. 4, number 3), followed by the Nevado de Toluca Volcano (Fig. 4, number 4). Lower connectivity was found between the Iztaccíhuatl-Popocatépetl-Zoquiapan volcanoes; the population of the Tláloc volcano was disconnected from the populations of the Iztaccíhuatl-Popocatépetl volcanoes, although these volcanoes are part of the same mountain chains (Fig. 4, number 1). Reserva de la Biósfera Santuario Mariposa Monarca (Fig. 4, number 5) is disconnected from the nearest volcano, the Nevado de Toluca Volcano, The *C. triseriatus* populations outside the mountain chains are disconnected (Fig. 4), mainly by a matrix of grasslands, agriculture and urbanisation.

## Discussion

According to ENM and the resistance surface, *C. triseriatus* populations have a highly fragmented distribution with low values of connectivity, mostly restricted within the *Abies-Pinus* forest of the mountain chains of the State of Mexico and Mexico City. The *Abies-Pinus* forests were highly important variables according to ENM, being *Abies* the first and *Pinus* the fourth most important variables. The Trans-Mexican Volcanic Belt has the highest amount of *Abies* forest (91.143%) and a great percentage of *Pinus* forest (29.657%) of the country, however these types of forests are scarce in the Trans-Mexican Volcanic Belt, where only 1.1% of *Abies* forest and 5.4% of *Pinus* forest cover the biogeographic zone. Therefore, it is essential to establish conservation plans to preserve this habitat, since good quality habitat maintains high levels of genetic diversity in the populations of *C. triseriatus* (Sunny et al. 2018).

Likewise, *Abies* forest is highly correlated with the *C. triseriatus* distribution, likely because these two species evolved together when this biogeographic province was formed in the Neogene; in fact, the uplifting of the Trans-Mexican Volcanic Belt is considered one of the most important forces driving the evolutionary history of several taxa (León-Paniagua et al. 2007; McCormack et al. 2008;

Bryson and Riddle 2012), including the *C. triseriatus* species (Bryson et al. 2011) and the *Abies religiosa* forest (Aguirre-Planter et al. 2000; Aguirre-Planter et al. 2012).

These species have adapted to high cold mountain environmental conditions (Sáenz-Romero et al. 2012). The second most important variable in determining the presence of the species was the minimum temperature of the coldest month and the third most important variable was the maximum temperature of the warmest month; these variables were important because *C. triseriatus* is an ectothermic species, adapted to low temperatures (Campbell and Lamar 2004; Sáenz-Romero et al. 2012). However, *C. triseriatus* has an optimal thermal range like other reptiles' species (Niewiarowski 2001; Rock et al. 2002; Sears 2005), between -1 °C and 27 °C; the higher temperatures of year are important in order to carry out essential activities like growth and reproduction (Sears 2005; Harvey and Weatherhead 2010); in high latitudes and/or elevations, in the colder months, there are important reductions in activity and resource acquisition resulting in slow growth and delayed maturation leading to lower body size in *C. triseriatus* and other reptiles' species (Blackburn et al. 1999; Martin 2002; Angilletta et al. 2004). *Crotalus triseriatus* is adapted to lower temperatures of the highest mountains of the continent (Campbell and Lamar 2004), therefore, we think that the increase in temperature caused by climate change will limit this species and others (*C. tlaloci*, *C. campbelli*, *C. armstrongi*, *Thamnophis scalaris*, *Pseudoeurycea leprosa*, *P. robertsi* and *Aquiloeurycea cephalica*) in their ability to shift distribution upslope, thereby increasing the possibility of its becoming extinct (Parra-Olea et al. 2005; Bryson et al. 2011; Velo-Antón et al. 2013; Bryson et al. 2014; González-Fernández et al. 2018; Sunny et al. 2019).

The ENM shows that *C. triseriatus* populations have a highly fragmented distribution for several reasons: one possible explanation is that the habitat, which this species prefers, is high mountain areas within the *Abies-Pinus* forests that are historically isolated (Aguirre-Planter et al. 2012). Likewise, it could be due to the loss and fragmentation caused by land use changes that have occurred in the lower areas of the study area. This zone has two of the major metropolitan areas of Mexico, as Valle de Mexico contains 2,557.4 people per km$^2$, which is one of the world's largest metropolitan areas (CONAPO 2010); also, 44.7% of this biogeographic zone is used for agriculture, although some *Crotalus* species are quite tolerant or can even benefit from small patches of crops, probably due to the small prey species that live there (Mociño-Deloya et al. 2008; Reinert et al. 2011; Wittenberg 2012). However, only those crops close to *Abies* forests seem to be suitable habitats for *C. triseriatus* (Mociño-Deloya et al. 2014). These forests provide the possibility for rattlesnakes to find different kinds of food, such as rodents, amphibians, lizards, birds and eggs (Mociño-Deloya et al. 2014).

Although there are stable populations in the agriculture fields, large rattlesnakes have insufficient refuges and a variety of vegetation cover to allow the exploitation of thermal gradients (Blouin-Demers and Weatherhead 2001; Hoss et al. 2010; Sunny et al. 2015). This lack of vegetation limits the growth of rattlesnakes (Mociño-Deloya et al. 2014). Therefore, it is necessary to leave areas of native vegetation in the agricultural areas (rocks, shrubs and trees).

It is also important that populations are not isolated in small patches of habitat (Frankham et al. 2005). The populations that are isolated in patches of agriculture with low levels of landscape connectivity break the natural dynamics of the rattlesnake's metapopulations (Sunny et al. 2015), increasing the loss of alleles and genetic variability through genetic drift and the increased possibility of inbreeding can translate to lower fitness of the individuals in the population, which can lead to increased population susceptibility to disease (Frankham et al. 2005; Townsend et al. 2009; Rulon et al. 2011) and the proliferation of fungal pathogens (Jacobson et al. 2000; Paré et al. 2003; Rajeev et al. 2009), including some that cause widespread mortality in free-ranging rattlesnakes populations (Cheatwood et al. 2003), thereby increasing the extinction risk (Newman and Tallmon 2001).

In order to preserve the populations of *C. triseriatus* that live in the matrix of agriculture and urbanisation, it is necessary to leave rocks, shrubs and pastures around agriculture fields and leave native trees in order to create shelters with different microhabitats that generate thermal gradients; it is important to avoid the burning of pastures, since, apart from killing the biodiversity that lives in these pastures (*C. triseriatus*: dusky rattlesnake, *Barisia imbricate*: Imbricate Alligator Lizard, *Sceloporus torquatus*: Torquate Lizard Mountain, *Dryophytes eximius*: Treefrog, amongst others), around 5–10% of overall air pollution mortalities are due to the burning of biomass (Giglio et al. 2013; Yadav and Devi 2018). Furthermore, it is critical to implement environmental education for the people in order to avoid further rattlesnake killings due to fear or because they believe that rattlesnake meat cures cancer (Monroy-Vilchis et al. 2008).

The populations found in the mountain ranges have moderate to low levels of connectivity, mainly in the mountains of Iztaccíhuatl-Popocatépetl-Zoquiapan volcanoes and the Biosphere Reserve Monarch Butterfly Sanctuary is totally disconnected from any other population of *C. triseriatus*. It can also be observed that areas of high suitability found in Sierra de las Cruces and the Corredor Biológico Chichinautzin are outside protected areas.

It would be important to carry out landscape genetic studies to find out how fragmentation and isolation of the populations could be affecting the populations of *C. triseriatus*. The only population genetics study was carried out in the Nevado de Toluca Volcano and the results showed that the populations present moderate to high levels of genetic diversity (Sunny et al. 2018); however, this study shows that this zone is also isolated from the other populations of the species.

In conclusion, the preservation of *C. triseratus* will require the increase and maintenance of the connectivity

amongst areas of habitation, as well as the protection of other species that harness these corridors. To maintain and improve positive results on conservation efforts, constant research is required on ecological traits and population parameters (e.g. connectivity, diversity) of this species, as well as predictive modelling to anticipate population dynamics under future climate change scenarios. Finally, it is important to conduct dissemination of information within the human populations that share the habitat with this species. Environmental education talks are expected to prevent the further killing of snakes out of fear or for medicinal or ritual purposes.

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